WALL STRUCTURE OF SOME AGGLUTINATED FORAMINIFERIDA

by J. W. MURRAY

ABSTRACT. Present knowledge of agglutinated wall structure and composition is briefly reviewed. Examination of 19 recent species shows the existence of three wall types: simple imperforate wall with an organic cement; complex alveolar imperforate wall with an organic cement; 'perforate' wall with a calcareous cement. It is concluded that more attention should be paid to wall structure and composition in descriptions of species and in taxonomy. Forms with a calcareous cement seem to be stenohaline marine or hypersaline and therefore useful indicators of environment.

WILLIAMSON (1858, p. xi) recognized and named the three main wall types seen in recent foraminiferids: agglutinated, porcellaneous, and hyaline. Then followed the classification by Carpenter, Parker, and Jones (1862) partly based on these characters, together with the presence or absence of pores. Since that time wall structure has held an important position in taxonomy.

Although there are many observations on agglutinated wall structure scattered through the literature, there have been no recent detailed studies (see Lindenberg 1967 for a review). Investigations using electron microscopy have been concentrated mainly on the porcellaneous and calcareous lamellar wall types. However, Jahn (1953) and Towe (1967) published micrographs taken with transmission electron microscopes and Murray (1971) has illustrated the surface texture of twenty-five species in seventeen plates of scanning electron micrographs.

The purpose of this paper is to present a brief review of the present state of knowledge of agglutinated wall structure and to compare with this the results obtained during the examination of nineteen recent species.

The present state of knowledge of agglutinated wall structure may be summarized as follows:

1. The wall consists of detrital particles held together by a cement secreted by the animal.
2. Many different kinds of detrital particles including organic debris (see Thalmann 1948) are used by different species. Some seem to show no selectivity (e.g. *Reophax curtus*, Smith and Kaesler 1970) while others are highly selective (see Hedley 1964). However, it is not uncommon for the grain size to vary from one part of the test to another or within the thickness of the wall (Lacroix 1931).
3. The cement may be entirely organic or it may be mineralized. Hedley (1963) found the organic material to be '. . . an acid mucopolysaccharide (protein linked with carbohydrate), with organically bound iron and, most probably, organically bound calcium'. Mineralization may involve calcareous or ferruginous deposits or both.
4. Cements mineralized with ferruginous material are known to contain the iron as ferric oxide (Hedley 1963; Towe 1967) in a fine-grained amorphous condition (Towe 1967).

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5. Cements mineralized with calcareous material contain microgranular calcite 5 to 10 μm in diameter (Wood 1949).
6. Pores, tubes, and alveolae have been recognized in some walls and these are lined with a thin organic layer (Moebius 1880; Nørvang 1966). In most described examples the pore tubes do not penetrate to the outer surface of the wall. The pore tubes commonly branch (Lacroix 1939).
7. Thin organic membranes around the detrital particles have been recognized by Nørvang (1966).
8. The ratio of detrital particles to cement is highly variable (Cushman 1929).
9. Some walls contain inter-grain spaces due to incomplete cementation (Bartenstein 1952, p. 315).

METHODS

Well-preserved specimens from Recent sediment were selected for study. Some were examined whole, others broken to reveal internal structures and still others were sectioned using the following method:

The specimens were placed on a metal stub (for use in the scanning microscope) together with a small piece of 'Lakeside' thermoplastic cement. The stub was then gently heated in a Bunsen flame to melt the Lakeside and allow it to penetrate into and around the specimens. After cooling individual specimens were manipulated into the desired orientation using a hot needle. Then they were carefully ground away (under a stereoscopic microscope) using a finely ground glass slide lubricated with water. The sections were then etched in 5% EDTA for periods ranging from ½ to 10 minutes.

All specimens were prepared for examination in the scanning electron microscope by coating them with a 40/60 mixture of gold/palladium in a vacuum coating unit.

The X-ray diffraction traces were made from bulk assemblages of each species.

The presence of ferric iron was inferred from the development of a prussian blue colour in specimens treated with a solution of potassium ferrocyanide in hydrochloric acid (2 gm in 100 mls of 1·75% HCl).

MATERIAL

Species	*Locality*
Saccammina atlantica (Cushman)	Shelf off Long Island, U.S.A.
Miliammina fusca (Brady)	Christchurch Harbour, England.
Cribrostomoides columbiense (Cushman)	Van Damme Beach, California.
Cribrostomoides crassimargo (Norman)	Shelf off Long Island, U.S.A.
Cribrostomoides jeffreysii (Williamson)	Western Approaches to English Channel.
Cyclammina cancellata (Brady)	Continental slope W. of English Channel.
Ammoscalaria pseudospiralis (Williamson)	Kattegat.
Textularia earlandi (Parker)	Celtic Sea.
Textularia sagittula (Defrance)	Western Approaches to English Channel.
Textularia sp.	Shelf off Trucial Coast, Persian Gulf.
Siphotextularia flintii (Cushman)	Celtic Sea.
Trochammina inflata (Montagu)	Christchurch Harbour, England.
Trochammina lobata (Cushman)	East coast, U.S.A.
Jadammina macrescens (Brady)	Christchurch Harbour, England.

Species	*Locality*
Gaudryina rudis (Wright)	Western Approaches to England Channel.
Eggerella advena (Cushman)	Shelf off Long Island, U.S.A.
Eggerella scabra (Williamson)	Western Approaches to English Channel.
Clavulina pacifica (Cushman)	Off Jeddah, Red Sea.
Martinottiella communis (D'Orbigny)	Western Approaches to English Channel.

RESULTS

Space limitations prevent a full description of each of the species studied so only a few species will be described in detail.

Forms having an organic cement. Saccammina atlantica has a unilocular test of variable form although it is commonly pyriform with an aperture at the narrow end. The wall is made up of a detrital quartz grains of variable size and shape (Pl. 99, fig. 1). Much of the wall is built of larger grains which span the entire thickness. These grains are closely fitted together with a separation of less than 1 µm along most of their edges (Pl. 99, fig. 2). However, complete fitting is not possible and the spaces are filled with a mosaic of progressively smaller grains (Pl. 99, figs. 4, 5). In these areas the wall is several grains thick. The surface of the wall is rough both on the outside (Pl. 99, figs. 1, 6) and on the inside (Pl. 99, fig. 5). There are no wall pores. Specimens placed in 5% EDTA or 1·75% HCl showed no reaction and it is concluded that the cement contains no $CaCO_3$.

Other species found to have a simple structure include *Eggerella advena*, *E. scabra*, *Cribrostomoides columbiense*, *C. crassimargo*, *C. jeffreysii*, *Textularia earlandi*, *Martinottiella communis*, *Trochammina lobata* and *Miliammina fusca*.

In *Ammoscalaria pseudospiralis* there is a clearly visible organic lining in the chambers (Pl. 99, fig. 7). This can also be seen in *Trochammina inflata*.

In many of these forms economy of cementation leads to small inter-grain spaces in the wall (first noted by Bartenstein, 1952) but no evidence has so far been seen to suggest that these are in any way pores.

Cyclammina cancellata has a complex labyrinthic wall structure (see Banner 1970, for the most recent description). The outer wall (epidermis) is imperforate and smoothly finished. The inner wall (hypodermis) is coarsely alveolar. It is known from previous studies that the cement is organic, with iron mineralization (Hedley 1963). In the present study it was found that the outer and inner wall surfaces and the linings of the alveolae are all completely bound with cement. Within the thickness of the wall the grains are only loosely cemented at their points of contact. No differences could be observed in specimens treated with acid so it is concluded that there is no calcite cement. However, some specimens have coccoliths among their detrital grains and the presence of such calcareous material may account for the calcium recorded in analyses by Brady (1884), Fauré-Fremiet (1911), and Vinogradov (1953). Hedley (1963) published an analysis of carefully cleaned specimens in which CaO was absent.

Forms having a calcareous cement. Clavulina pacifica starts with a triserial juvenile portion and then becomes uniserial (Pl. 100, fig. 1). The outer surface of the wall shows the presence of larger detrital grains, including quartz, amphibole, and sponge spicules, and smoother areas of cement and fine detrital grains (Pl. 100, fig. 2). There are no pores penetrating the outer surface. By contrast the inner surface is smoothly finished and shows many pores generally 2 to 3 µm in diameter and closed with an organic membrane (Pl. 100, fig. 3). Broken sections reveal that the pores extend almost through the wall but end blindly just beneath the outer surface (Pl. 100, fig. 4). Specimens impregnated with 'Lakeside', sectioned and etched with 5% EDTA reveal the complexity of the pores. The latter, now filled with 'Lakeside', are seen to be cylindrical tubes through much of the wall but they branch just beneath the outer surface (Pl. 100, fig. 5). Moreover, they appear to be lined with an organic layer which also extends between the pores as vertical partitions (Pl. 100, fig. 6). Pores also extend into the septa but do not penetrate to the apertural side.

Apart from the organic material observed in the wall, the cement consists of calcite (confirmed by X-ray diffraction). It occurs as small units commonly less than 0·5 µm in size (Pl. 100, fig. 7) and sometimes as elongate rods on the outer surface (Pl. 100, fig. 8). Much of the inner part of the wall seems to consist of calcite cement, the detrital grains being mainly in the outer part.

Brief etching with acid causes removal of some of the cement from the outer surface thus allowing the ends of the pore-tubes to be seen. A similar perforate appearance of the test results from gentle abrasion.

Textularia sagittula shows similarities with *Clavulina pacifica* particularly in having a calcite cement and blindly ending pore tubes. The detrital grains are mainly quartz and they are only loosely fitted together on the outer surface, the intervening spaces being occupied with calcite cement (confirmed by X-ray diffraction). Sections impregnated with 'Lakeside' and etched in acid reveal an anastomosing network of pore tubes which end blindly beneath the outer surface of the wall (Pl. 99, fig. 8). The calcite cement occurs as more or less equigranular grains 0·5 to 0·7 μm in size.

Gaudryina rudis likewise has an agglutinated wall with a calcareous cement. The outer surface is rough, due to detrital shell debris incorporated on the sides of the test, although the apertural face is smooth (see Murray, 1971, pl. 14). The inner surface of the chamber side wall is perforated by pores 7 to 8 μm in diameter. These tubular pores end blindly beneath the outer surface of the wall although etched and abraded specimens give the appearance of being perforate. The septa and apertural face lack pores and tubes.

Other species having this type of wall with blindly ending pores are *Textularia* sp. from the Persian Gulf and *Siphotextularia flintii.*

Ferric iron. With the exception of *Cribrostomoides columbiense*, *Cyclammina cancellata*, and *Ammoscalaria pseudospiralis*, all the species were tested for ferric iron and all reacted positively although with different intensities. In the case of the forms with calcareous cements the test was destroyed by the acid solution and the colouration was developed in the residual organic framework.

DISCUSSION

The results presented here agree, in general, with those of previous workers, but there are some differences.

The presence of pores in *Textularia* was first described by Carpenter, Parker, and Jones (1862, p. 191). A more complete description by Moebius (1880) recorded the presence of a 'chitinous' lining in the chambers and in the pore tubes. He also noted that the pores reached the surface only in the younger chambers. Lacroix (1931) studied the same species as Moebius, *T. agglutinans* d'Orbigny. He observed that the pore tubes bifurcate close to the outer surface and stated that they opened on to the surface through very small pores. He also noticed that the inner organic lining covered the pores as well as the chamber wall. Reyment (1969) recognized 'ultrapores' in *Textilina mexicana* (Cushman) but he gave no information about the passage of these pores through the wall.

In the present study no evidence could be found of pore openings at the outer surface except where the test had clearly suffered abrasion or etching with acid. In *Clavulina pacifica* and *Gaudryina rudis* the pore-bifurcations beneath the wall surface have a diameter of approximately 1 μm and if they opened on the surface they should be clearly visible. It seems certain that they are closed either by an organic membrane or by calcite cement.

EXPLANATION OF PLATE 99

Figs. 1–6. *Saccammina atlantica* (Cushman) 1, General view, × 120. 2, close fit of two quartz grains, × 1150. 3, The aperture, showing large and small quartz grains, × 750. 4, Close fit of small grains between large detrital grains, × 1500. 5, Detail of inner side of wall showing small grains filling the gaps between the larger grains, × 650. 6, Broken section of wall, × 1270.

Fig. 7. *Ammoscalaria pseudospiralis* (Williamson) showing organic lining (o) on inside of wall, × 1300.

Fig. 8. *Textularia sagittula* Defrance. Impregnated and etched section of wall showing anastomosing pore tubes (p) and quartz grains (q) on the outer side, × 1400.

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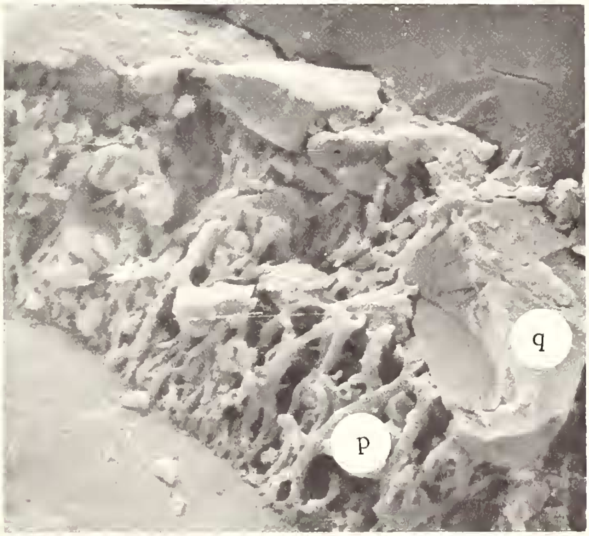

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MURRAY, agglutinated foraminifera

Nørvang (1966) studied *Textularia sagittula* Defrance and found the walls to be imperforate. Lacroix (1931) studied what he called the same species and found the pores to be present but small (1 μm in diameter).

The data on pores in agglutinated walls with a calcareous cement is summarized below:

1. They may be tubular with bifurcations near the outer wall surface or they may form an anastomosing network throughout the wall.
2. They end blindly just beneath the outer wall; no definite pore openings have been observed on the outer surface in the present study.
3. The pores are lined with a thin organic membrane.
4. They are closed with an organic membrane on the inside of the chamber and possibly also at the outer ends.
5. They are normally developed mainly in the chamber walls on the sides of the test. They are less well developed or are absent in the apertural face and in the septa.
6. In *Clavulina pacifica* the pores form 25% of the volume of the wall.

The pores of agglutinated walls were considered by Reiss (1963) to be different from those of calcareous lamellar foraminiferids because they are curved. Perhaps the most distinctive features are that they commonly branch and sometimes anastomose. In calcareous lamellar foraminiferids the pores are maintained even during the addition of further wall layers (see Hansen and Reiss 1971 for illustrations). By contrast, in agglutinated foraminiferids the wall is non-lamellar and each chamber wall is secreted as a single event.

All the forms with pores seem to be stenohaline marine or hypersaline species which are presumably in osmotic equilibrium with their environment. The forms with an organic cement not mineralized with calcareous material lack pores. Marszalek, Wright, and Hay (1969) have suggested such a test '. . . offers good refuge to the foraminifer under times of stress, and allows time for osmoregulatory adjustment to the new conditions'. This could account for the presence of such forms in hyposaline environments.

The wall of *Cyclammina cancellata* presents a special case. Although the hypodermis contains alveolae these are in complete communication with the chamber lumen and they are not crossed by an organic membrane at the inner ends. They do not therefore compare with the pores discussed above and the wall of *Cyclammina* must be regarded as imperforate.

EXPLANATION OF PLATE 100

Figs. 1-8. *Clavulina pacifica* Cushman. 1, General view, ×70. 2, Detail of wall texture showing detrital grains (g), ×220. 3, Inner side of wall with pores covered by an organic membrane, ×4000. 4, Broken section of wall showing the pore tubes ending blindly at the outer side, ×1350. 5, 6, Impregnated and etched section of wall showing the pore tubes bifurcating and ending blindly below the outer surface, ×1400, in 5 and transverse sections of the pore tubes and associated organic membranes, ×670, in 6. 7, Broken section of wall showing closely packed pore tubes built mainly of cement, ×3400. 8, Detail of outer wall surface showing elongate cement crystals between detrital grains, ×3400.

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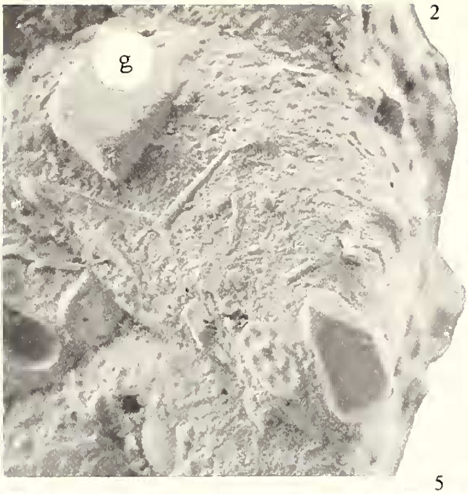

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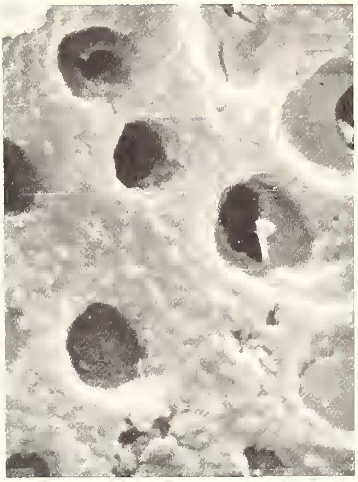

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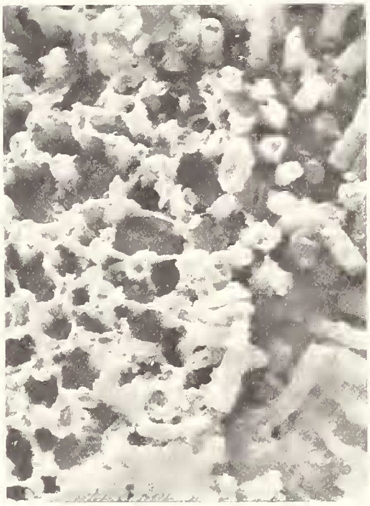

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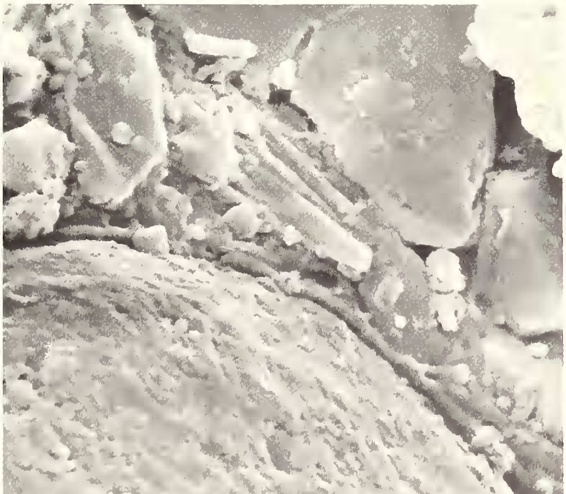

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WALL STRUCTURE AND CLASSIFICATION

In the classification adopted in the Treatise (Loeblich and Tappan 1964) nearly all agglutinated forms are placed in the suborder Textulariina. This includes the superfamily Ammodiscacea, in which the wall is said to be 'agglutinated, simple, or labyrinthic', and the superfamily Lituolacea, 'wall siliceous or agglutinated, with calcareous, siliceous, or ferruginous cement'.

At lower taxonomic levels the information is often lacking in detail or at variance with the present observations. For the Saccamminidae the wall is not mentioned. The family Lituolidae has 'wall agglutinated, with calcareous cement or microgranular calcite, interior simple to labyrinthic, epidermal layer imperforate'. Genera of this family which have been found in the present study not to have a calcareous cement include *Cribrostomoides*, *Cyclammina*, and *Ammoscalaria*. The family Textulariidae has 'wall agglutinated'. For *Textularia* it is said to be 'simple'. The wall of *Siphotextularia* is not described. The family Trochamminidae just has 'wall agglutinated'. The same is true of the Ataxophragmiidae. *Gaudryina* has no wall description, *Eggerella* has 'wall finely agglutinated on pseudochitinous base, may be of calcareous particles in calcareous cement'. This disagrees with the results presented here. *Clavulina* has 'wall agglutinated with much calcareous cement'. *Clavulina pacifica* agrees with this. *Martinottiella* has 'wall finely agglutinated'. Thus, of the four Ataxophragmiidae examined two have an organic cement and no pores (*Eggerella* and *Martinottiella*) and two have a calcareous cement and pores (*Gaudryina* and *Clavulina*).

This raises the question of the value of the wall structure and cement composition as taxonomic features. In a general sense the agglutinated wall structure is clearly useful. However, should more notice be taken of the detailed structure? Since the cement is secreted by the foraminiferid it must surely be of greater taxonomic value than the nature of the detrital particles gathered from the sediment. The kind of cement is a reflection of the physiology of the animal. This must be at least of equivalent importance to the nature of coiling or the arrangement of the chambers. Unfortunately, in the majority of descriptions of agglutinated species a full description of the wall structure and composition is omitted.

ECOLOGICAL SIGNIFICANCE

Foraminiferids with agglutinated walls are known to be particularly common in the deep sea, in cold shelf seas, and in shallow and intertidal hyposaline waters. There is now clear evidence that the nature of the cement is of ecological significance.

Pokorny (1958) suggested that forms with an organic cement characterize cold water. Lindenberg (1966) inferred that in the Dogger (Jurassic) of south west Germany the forms with a calcareous cement lived in more marine waters than those with an organic cement.

The results of the present study support Lindenberg's view. All the examined species having a calcareous cement come from normal marine or hypersaline environments (Western Approaches to the English Channel, Celtic Sea, Persian Gulf, Red Sea). Those with a simple wall and an organic cement are found in hyposaline marshes and lagoons (*Trochammina inflata*, *Jadammina macrescens*, *Miliammina fusca*), hyposaline shelf seas (*Saccammina atlantica*, *Cribrostomoides crassimargo*, *Eggerella advena*), and normal marine shelf seas (*Martinottiella communis*, *Textularia earlandi*, *Eggerella scabra*). Thus they occur in many different environments. The only form with a complex alveolar wall studied here is characteristic of the continental slope with sigma-t values of 27·7 (see Banner 1970, p. 244).

The restriction of forms with a calcareous cement to normal marine and hypersaline shelf seas should prove useful in helping to interpret the palaeoecology of fossil assemblages.

CONCLUSIONS

The nineteen species discussed here are hardly representative of the hundreds of agglutinated species but the results nevertheless have some interest. Clearly there are more types of agglutinated wall structure to be discovered. At the taxonomic level many more species need to be investigated in detail and then it will be possible to emend generic and family descriptions and groupings. From the ecological point of view the nature of the cement appears to be important and controlled laboratory experiments should be carried out to gain further knowledge.

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Discussion on Dr. Murray's paper:

Green: Is there any organic membrane lining the pores?

Murray: Yes. This is something which I omitted to mention in the talk. I have some additional micrographs which show organic walls running between the pores perpendicular to the chamber surface, so the whole of the inside of the wall has a mesh-work of organic material, and this presumably replaces the calcitic cement.

Green: Filling the gaps in?

Murray: Or else the opposite; it is trying to reduce the density of the wall, because the density of calcite is great with respect to sea water.

Rood: Is the cement of such a nature that it could conduct an ion flow through the cement into the inner structures?

Murray: I do not think that any of the work I have done so far could prove this, but it seems strange if the animal felt the need to transport material through the cement, when it has tubular pores in the wall. The odd thing about these pores is that they only occur in the sideways facing parts of the test—they don't occur in the final face of the test, the one that is held down to the sea floor where the animal is living.

Daniels: Perhaps in life the grains over the ends of the pores are loose, and the animal can create some sort of exit.

Murray: I have taken many pictures of the outer surface, and the cement always comes round the grains holding them in place very firmly.

Sylvester Bradley: How do you think the cement got there?

Murray: When the animal secretes its skeleton, there would have to be places where the pseudopodia came out.

Sylvester Bradley: You don't think that these pores were where the pseudopods came out?

Murray: I must admit that that is a good point. But one has to ask why the pseudopods covered the ends of the pores with a membrane after withdrawing into the chamber.